Description of two new genera and species of Eriococcidae (Hemiptera: Coccoidea) from southern South America

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Abstract

Two new genera of Eriococcidae, *Intecticoccus* Kondo and *Orafortis* Hardy, each with a new species (*I. viridis* Kondo and *O. luma* Hardy), are described and illustrated based on the adult females. *I. viridis* was collected on *Nothofagus antarctica* (Nothofagaceae) in Argentina and Chile, and *O. luma* was collected in Chile on *Amomyrtus luma* (Myrtaceae). Based on a phylogenetic analysis of SSU rDNA (18S) sequence data, *I. viridis* and *O. luma* are placed within the Gondwanan group of eriococcids (*sensu* Cook & Gullan 2004), which also includes other *Nothofagus*-feeding genera such as *Chilechiton* Hodgson & Miller, *Chilecoccus* Miller & González and *Madarococcus* Hoy. Major genera within the Gondwanan group that feed on other plant groups include *Lachnodius* Maskell, *Opisthoscelis* Schrader and some species currently assigned to *Eriococcus* Targioni Tozzetti. We consider that *I. viridis* and *O. luma* are each sufficiently distinct from other named taxa to warrant erection of two new genera. DNA data do not support a relationship of *Chilechiton* with the New Zealand genus *Eriochiton* Maskell. A revised taxonomic key to the adult females of Eriococcidae known from Chile is provided.

Key words: *Amomyrtus*, Argentina, Chile, Eriococcidae, *Intecticoccus*, new genus, new species, *Nothofagus*, *Orafortis*, scale insects, phylogenetic analysis

Resumen

Dos nuevos géneros de eriocóccidos, *Intecticoccus* Kondo e *Orafortis* Hardy, cada uno con una nueva especie (*I. viridis* Kondo e *O. luma* Hardy) son descritos e ilustrados basandose en la hembra adulta. *Intecticoccus viridis* fue colectada sobre *Nothofagus antarctica* (Nothofagaceae) en Argentina y Chile y *O. luma* fue colectada en Chile sobre *Amomyrtus luma* (Myrtaceae). En base de un analysis filogénico obtenido por data de sequencias del SSU ADNr (18S), *I. viridis* y *O. luma* se



ubican dentro del grupo Gondwánico de eriocóccidos (sensu Cook & Gullan 2004), cual también incluye otros géneros que tienen como hospederos a árboles del género Nothofagus tales como Chilechiton Hodgson & Miller, Chilecoccus Miller & González y Madarococcus Hoy. Dentro del grupo Gondwanánico también hay especies que se alimentan de otros grupos de plantas, tales como algunas especies actualmente incluidas en el género Eriococcus Targioni Tozzetti, y especies en los gèneros Lachnodius Maskell y Opisthoscelis Schrader. Nosotros consideramos que I. viridis y O. luma son suficientemente distintas de otras taxa para ser colocadas en dos nuevos géneros. El data obtenido por el ADN no apoya la relación de Chilechiton con el género Eriochiton Maskell de Nueva Zelanda. Se provee una clave taxonómica revisada para las hembras adultas de la familia E riococcidae de Chile.

Introduction

The Eriococcidae comprises an assemblage of scale insects that are especially diverse in the southern hemisphere (Miller & Gimpel 2000, 2006), except Africa (Gullan et al. 2006). The non-monophyly of this family was suggested by Cox & Williams (1988) based on assessment of morphological features, and later confirmed by phylogenetic analysis of adult males (Hodgson 2002) and molecular data (Cook et al. 2002; Cook & Gullan 2004). Molecular data suggest that most eriococcids sensu lato (i.e., including at least Dactylopiidae, Beesoniidae and Stictococcidae) belong to three major groups — the acanthococcid clade with a worldwide distribution, the beesoniid-stictococcid-Eriococcus sensu stricto (BSE) clade with an Old World distribution, and the Gondwanan clade including Australian and New Zealand taxa, many of which feed on Myrtaceae but also including the Nothofagus-feeding Madarococcus Hoy (Cook & Gullan 2004). Cook & Gullan (2004) suggested that South American eriococcids, in particular, were required to test the boundaries of this latter clade. The eriococcid faunas of Australia and New Zealand are known to be extremely species rich and include some morphologically highly specialized taxa (Hoy 1962a; Miller & Gimpel 2000; Gullan et al., 2005). South American eriococcids include some similarly specialized and unusual taxa, but only about 50 species have been described from the whole of the Neotropical region (Ben-Dov et al. 2006) and no DNA sequence data have been published.

To date, 22 species of eriococcids *sensu lato* have been recorded from Argentina (15 species) and Chile (14 species), of which 10 species feed on *Nothofagus* (Nothofagaceae) (Miller & González 1975; González 2000; Miller & Gimpel 2000, 2006; Hodgson & Miller 2002; Ben-Dov *et al.* 2006). Despite the close proximity of the two countries, Argentina and Chile currently are known to share only seven species of Eriococcidae, all of which occur on *Nothofagus* except the introduced *Eriococcus araucariae* Maskell. Although the preponderance of eriococcid species on *Nothofagus* may reflect sampling bias, species of this tree genus dominate the temperate forests of these two countries (Veblen *et al.* 1996) and provide abundant and long-lived hosts for phytophagous insects (McQuillan 1993).

The eriococcids of the Nothofagus forests of Chile and bordering Argentina include

morphologically unusual genera such as *Chilechiton* Hodgson & Miller on *N. antarctica* and *N. dombeyi*, *Chilecoccus* Miller & González on *N. dombeyi* and *Eucryphia cordifolia* (Cunoniaceae), *Icelococcus* Miller & González on *N. antarctica*, *N. dombeyi*, *N. obliqua* and *Lithraea caustica* (Anacardiaceae), and *Stibococcus* Miller & González on *Myrceugenia bridgesii* (Myrtaceae) (Miller & González 1975; González 2000; Hodgson & Miller 2002). Of the above, only *Chilechiton* is restricted to *Nothofagus*.

It has been suggested that there is a close association between the eriococcids of Chile and those of New Zealand (Miller & González 1975; Hodgson & Miller 2002). For example, Hodgson and Miller (2002) placed *Chilechiton* as sister to the endemic New Zealand genera *Eriochiton* Maskell and *Neoeriochiton* Hodgson in the tribe Eriochitonini. However, none of the studies to date have sampled extensively from other geographic areas nor has strong support been recovered for New Zealand/Chile relationships, to the exclusion of others.

In comparison to the relatively well-documented New Zealand eriococcid fauna (Hoy 1962a; Hodgson 1994; Hodgson & Henderson 1996; Henderson 2006), there are only three taxonomic papers on the eriococcids of Chile and most collecting has targeted *Nothofagus* (Hoy 1962b; Miller & González 1975; Hodgson & Miller 2002). Another host-plant taxon with a South American-Australasian biogeographic connection is Myrtaceae (Sytsma *et al.* 2004), with 26 species in nine genera from Chile (Landrum 1998) and 73 species in 24 genera from Argentina (Zuloaga & Morrone 1999). Almost all the myrtaceous genera found in Chile occur also in Argentina. Although at least 12 species in six eriococcid genera have been described from Myrtaceae elsewhere in South America, primarily Brazil, only one species of eriococcid has been recorded from this plant family in Chile and only two species are known from Myrtaceae in Argentina (Ben-Dov *et al.* 2006; Miller & Gimpel 2006). This lack of taxonomic knowledge of Chilean and other Andean eriococcids is an impediment to understanding their relationships to taxa in other Gondwanan regions.

Here we describe a new species and genus of *Nothofagus*-feeding eriococcid from Chile and Argentina on the leaves of *N. antarctica*, locally known as ñirre, and a new species and genus of eriococcid from the stems of the myrtaceous tree *Amomyrtus luma* in Chile. We describe and illustrate the adult female of each species, and provide a revised key to the eriococcid species of Chile based on the adult females. We use DNA sequence data from a nuclear ribosomal gene to examine the relationships and confirm the distinctness of the two new genera.

Materials and methods

Slide-mounts were prepared using the method discussed by Gullan (1984). Taxonomic measurements were taken under a compound microscope with an ocular micrometer. All available specimens were measured for each species. The illustration of the adult female of

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each species was prepared based on multiple specimens and with the assistance of a camera lucida attached to a compound microscope. Each illustration follows the typical style as adopted for scale insects, with the venter depicted on the right side, and the dorsum on the left. Important details of the specimen are enlarged around each illustration, but are not proportional to each other. The morphological terms for Eriococcidae follow those of Miller & McKenzie (1967) and Williams (1985) with the modifications given by Gullan & Vranjic (1991). The term microduct is used here to describe the peculiar ventral microtubular ducts found in *Intecticocccus*, which are unusual in the Eriococcidae and resemble the typical coccid microducts. The terms "bilocular pore" (Gullan and Vranjic 1991; Gullan and Strong 1997; Kondo *et al.* 2004) and "cruciform pore" (Miller and McKenzie 1967; Williams 1985) both have been applied to an oval secretory structure with a slit-like orifice, appearing to be composed of 2 loculi separated by either a weak transverse septum, or a pair of smaller loculi forming a small notch perpendicular to the long axis of the orifice. We have used the term "bilocular pores" to refer to these pores, although some bilocular pores appear more cruciform than others.

Recent collecting in Chile has provided the opportunity to extract DNA and perform a preliminary phylogenetic analysis for several Chilean taxa. Here we investigate relationships among a subset of eriococcids using DNA sequence data with the aim of establishing that two undescribed species from Chile and Argentina are sufficiently distinct from other named taxa to warrant erection of two new genera. We selected species to represent the three eriococcid clades (acanthococcid, BSE and Gondwanan) recovered in a previous molecular analysis (Cook & Gullan 2004) plus a representative of each available Chilean genus including, if possible, the type species (Table 1). DNA sequences for seven eriococcid species were available on GenBank from previous work (Cook *et al.* 2002; Cook & Gullan 2004) and sequences were generated for the first time for six Chilean species, including the two new species described in this paper. DNA voucher specimens for these 13 species are deposited in the ANIC and BME (see below for depository acronyms).

DNA extraction and PCR protocols followed those of Cook & Gullan (2004). We amplified an approximately 600 bp fragment of the small subunit ribosomal RNA gene (SSU rDNA, 18S) using primers 2880 (Tautz *et al.* 1988) and B- (von Dohlen & Moran 1995). Sequences were edited in Sequencher v4.5 (Gibbs & Cockerill 1995) and aligned by eye using Se-Al (Rambaut 1996). Phylogenetic analyses were undertaken using MrBayes v3.1 (Ronquist & Huelsenbeck 2003). We used a GTR+I+G model and ran two simultaneous analyses for three million generations and checked for convergence. Trees saved during the burnin period (500,000 generations) were discarded prior to further analyses. The expansion regions of SSU rDNA show extensive length variation, making alignment and assessment of homology among eriococcids difficult. Analyses were therefore run with and without these ambiguously aligned regions to assess whether choice of alignment affected the estimated phylogenetic relationships.



ANIC	Australian National Insect Collection, CSIRO Entomology, Canberra, Australia		
BME	Bohart Museum of Entomology, University of California, Davis, U.S.A.		
BMNH	The Natural History Museum, London, U.K.		
IMLA	Fundación e Instituto Miguel Lillo, Universidad Nacional de Tucumán,		
	Tucumán, Argentina		
MLPA	Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina		
MNNC	Museo Nacional de Historia Natural de Chile, Santiago, Chile		
USNM	National Museum of Natural History Entomological Collection, Washington,		
	DC., U.S.A. (Coccoidea collection held at USDA, Beltsville, Maryland)		

TABLE 1. Specimens of Ericoccidae used in the phylogenetic study (*indicates that the species is the type of its genus, except that *E. aceris* is the type species of *Acanthococcus* Signoret).

Species	Voucher Code/ GenBank	Collection	Host-plant species
	No. (Depository)	country	
*Chilechiton lynnae Hodgson & Miller	LGC00585 (BME)	Chile	Nothofagus antarctica
*Chilecoccus sp. nr browni Miller & González	LGC00580 (BME)	Chile	Nothofagus dombeyi
Eriochiton spinosus (Maskell)	Echit1/AY795547 (ANIC)	New Zealand	Griselinia littoralis
*Eriococcus aceris (Signoret)	acer1/AY795539 (ANIC)	Hungary	Acer campestre
*Eriococcus buxi (Boyer de Fonscolombe)	buxi1/AY795513 (ANIC)	France	Buxus sempervirens
Eriococcus eucalypti Maskell	erioFL1/AY795531 (ANIC)	Australia	Leucopogon parviflorus
<i>Eriococcus eurythrix</i> Miller & González	LGC00581 (BME)	Chile	Nothofagus obliqua
*Icelococcus nothofagi Miller & González	LGC00583 (BME)	Chile	Nothofagus nitida
*Intecticoccus viridis Kondo sp. nov.	LGC00317 (BME)	Chile	Nothofagus antarctica
Madarococcus viridulus Hoy	LGC00161/AY795529 (ANIC)	New Zealand	Nothofagus fusca
Madarococcus sp. 'Nc'	ErioNc1/AY795528 (ANIC)	Australia	Nothofagus cunninghamii
*Orafortis luma Hardy sp. nov.	LGC00579 (BME)	Chile	Amomyrtus luma
Scutare lanuginosa Hoy	ScutA/AY795548 (ANIC)	New Zealand	Pseudopanax arboreus

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Results and discussion of the molecular analysis

The aligned region used for analysis comprised 614 bp (106 variable characters) when the whole fragment was included, and 543 bp sites (70 variable characters) when regions of ambiguous alignment were excluded. There was no base composition bias among taxa.

The phylogram is presented as unrooted (Fig. 1) but the most probable position of the root, as determined by bootstrapped maximum parsimony and neighbour-joining, is indicated by an arrow. Previous analyses have determined that the three eriococcid clades sampled here are monophyletic, but that estimated relationships among the three groups is dependent on the choice of gene and, to a lesser extent, the outgroup used. Here, only the placement and extent of divergence of the Chilean taxa is of concern and each of the six Chilean species falls strongly with one of the three previously identified groups of eriococcids.

Bayesian analysis of the complete data set, and with ambiguously aligned regions excluded (Fig. 1), recovered the three eriococcid clusters (acanthococcid, BSE and Gondwanan) with high support (PP =0.95). *Icelococcus nothofagi* was the only Chilean taxon to fall within the acanthococcid clade, which also includes New Zealand genera *Eriochiton* and *Scutare* Brittin. The remaining Chilean taxa (*Chilechiton, Chilecoccus, Intecticoccus* Kondo gen. nov. and *Orafortis* Hardy gen. nov.) fall within the Gondwanan clade but do not form a monophyletic group. The branch lengths and inferred relationships in Figure 1 indicate that *Intecticoccus* and *Orafortis* are each as genetically distinct in the conserved SSU rRNA gene as other currently recognized genera from Chile. These results also suggest that *Chilechiton lynnae* Hodgson & Miller (Gondwanan clade) is not closely related to the New Zealand taxon *Eriochiton* (acanthococcid clade), contrary to the hypothesis of Hodgson & Miller (2002).

Taxonomy

Intecticoccus Kondo gen. nov.

Type species: *Intecticoccus viridis* Kondo, **sp. nov.**, by present designation.

Generic description of adult female

Live appearance: Body either round or tapering towards posterior end, becoming ventrally concave and only slightly dorsally convex. Dorsum covered by a thin layer of transparent wax. Insects shiny, not producing a felted cover.

Unmounted material: Body elongate oval, segmentation distinct ventrally on abdomen.

Eyespots present. Antennae with 6 (rarely 5) segments. Tentorial box well developed, labium 3-segmented, with 8 pairs of hair-like setae: 2 pairs on basal segment, 1 pair on

median segment, and 5 pairs on apical segment. Legs well developed; tarsal and claw digitules both slender and knobbed; claw without a denticle, translucent pores small, present on hind coxae only. Anal lobes well developed, sclerotized, plate-like, without medial teeth. Triangular accessory plate absent from anterior base of anal plates. Anal ring with 8 setae and irregular row of wax pores. Suranal setae spinose.

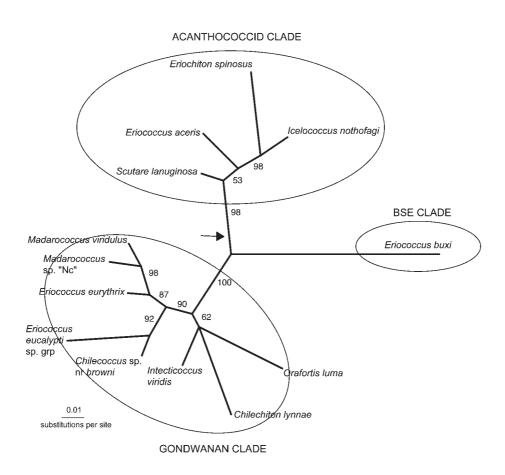


FIGURE 1. Unrooted phylogram of Bayesian consensus tree based on SSU rDNA; numbers next to nodes are the Bayesian posterior probabilities; the three outlined and named eriococcid groups are after Cook & Gullan (2004); the arrow indicates the most probable root of the tree; BSE refers to the beesoniid-stictococcid-*Eriococcus* clade.

Dorsum: Derm membranous, with areolations, becoming slightly sclerotized around margins in older specimens. Setae short, sharply to bluntly spinose. Enlarged setae absent, all setae minute. Dorsal macrotubular ducts, multilocular pores, bilocular pores and simple pores absent. Microtubular ducts present, scarce, with septum, scattered on dorsum.

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Venter: Ventral setae short, sharply spinose. Ventral macrotubular ducts absent. Ventral microducts present, each with a well-developed inner ductule, duct opening with a distinct septum. Multilocular pores restricted to venter, each mostly with 5-loculi. Spiracular pores similar in structure to rest of multilocular pores but smaller; pores associated with anterior spiracles extending to margin; pores associated with posterior spiracles clustered around peritreme and not extending to margin. Bilocular pores entirely absent.

Etymology. The genus name *Intecticoccus* is composed of the Latin adjective "*intecti*" meaning uncovered or naked, after the naked appearance of the eriococcid in life and the ending "*coccus*" commonly used in scale insect names.

Notes. Immature stages are not known for this genus and no male tests or cocoons have been seen. The female is oviparous, with developing eggs under her body.

Intecticoccus viridis Kondo sp. nov. (Figs 2A–B, 3)

Type material. HOLOTYPE, adult female. **CHILE:** IX region, Villarrica, Fundo Flor del Lago, 39°09'S, 72°06'W, 15.xii.2003, coll. T. Kondo, ex leaf of *Nothofagus antarctica* (ñirre) (MNNC). **PARATYPES: CHILE:** same data as holotype, 29 adult females (13 BME + 4 BMNH + 8 MNNC + 4 USNM); **ARGENTINA:** Parque Nacional Lanín, Lago Queñi, 22.i.1997, coll. P.J. Gullan, ex leaves (mostly undersides) of *N. antarctica*, 6 adult females (1 BME + 1 IMLA + 3 MLPA + 1 USNM); c. 5 km W. of Villa Mascardi, 31.xii.1996, coll. P.J. Gullan, ex underside leaves of *N. antarctica*, 7 adult females (2 BME + 3 IMLA + 1 MLPA + 1 USNM).

Description of adult female (n = 43)

Live appearance. Found on leaves, mostly undersides. Insects covered by a thin layer of glassy wax, not producing a test. Body of young adult female yellowish-green, shiny, often with a yellowish or brownish mid-longitudinal line (Fig. 2A). Older specimens becoming brown in color, beginning around mid dorsum (Fig. 2B). Venter becoming concave during egg laying period, sheltering many eggs.



FIGURE 2. A, Young adult females of *Intecticoccus viridis* Kondo **sp. nov.** on leaf of *N. antarctica* (Photo by Cristián Muñoz); B, Mature adult females of *I. viridis* **sp. nov.** on leaves of *N. antarctica* (Photo by P.J. Gullan); C, Alcohol-preserved adult female of *Orafortis luma* Hardy **sp. nov.** in test (sac) on twig axil of *Amomyrtus luma* (Photo by T. Kondo).

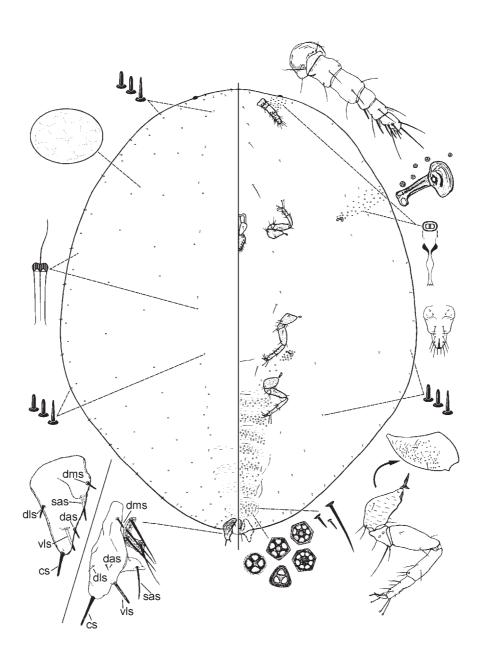


FIGURE. 3. Adult female of *Intecticoccus viridis* Kondo **sp. nov.** Anal lobe setae: (dls) dorsolateral lobe setae; (dms) dorsomedial lobe seta; (das) dorsoapical lobe seta; (cs) caudal seta; (vls) ventral lobe setae; (sas) suranal setae.

Mounted material. Body oval to elongate oval, slightly tapering towards posterior end (Fig. 3). Body 1.8–3.4 mm long, 1.7–2.9 mm wide. Eyespots present as dark spots anterior to or approximately level with antennal scapes, each 20–25 µm wide. Antennae 175–195 µm long, 6-segmented (one specimen with left antenna with 5 segments); generally located far from mouthparts on area close to anterior margin; 4 hair-like setae (trichoid

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sensilla) on segment I, 3 hair-like setae on segments II and III, respectively, 1 fleshy seta on segment IV, 5 hair-like setae and 1 fleshy seta on segment V, about 5 hair-like setae and 3 fleshy setae on segment VI. Tentorial box 113-138 μm long, 80-118 μm maximum width. Labium 105-113 μm long, 65-93 μm wide across base. Legs: all legs with trochanter + femur 130–150 µm long, tibia + tarsus 135–160 µm long; tarsal digitules 38-45 μm long, knobbed apex ca. 5 μm wide; claw digitules 28-33 μm long, knobbed apex ca. 2 µm wide; translucent pores present only on dorsal side of hind coxae, none on ventral side; microtrichia on ventral side of all coxae. Spiracular peritremes each 23-28 μm wide. Anal lobes variable in shape, conical to triangular depending on orientation, often with a long medial extension arising from ventral side of inner margin, each plate 130-155 µm long, 55-80 µm wide. Anal lobe setae difficult to interpret due to variable shape of lobes and their position when slide-mounted, however, number and relative position of setae typical of eriococcids. Each lobe with 6 setae: dorsolateral lobe setae (dls) 7-13 µm long, dorsomedial lobe seta (dms) 37-50 µm long, dorsoapical lobe seta (das) 11–15 μm long, caudal seta (cs) 38–55 μm long, ventral lobe setae (vls) 25–37 μm long. Anal ring 45–55 µm long, 53–65 µm wide, each seta 75–100 µm long. Suranal setae (sas) sometimes appearing ventral on anal lobes but apparently on a sclerotized medial extension of anal lobe, each seta 25-55 µm long.

Dorsum: Derm with microtrichia on last 4 abdominal segments, on area between each pair of parallel longitudinal setae. Setae each 2.5–6.5 μm long, found in 2 or 3 parallel longitudinal rows on mid dorsum and around body margin. Microtubular ducts scarce, in about 4 longitudinal rows on each side of body, usually with a microduct present near each dorsal seta, diameter of duct rim 2.5–3.0 μm.

Venter: Derm membranous; microtrichia present on mid areas of all abdominal segments. Ventral setae bluntly to sharply spinose, longer setae 25–70 μm long, shorter setae each 3–25 μm long, intermixed in segmental rows on mid areas of abdomen, scarce elsewhere, with one long seta associated with each mid and hind coxa; with 4 pairs of setae in a longitudinal line extending from interantennal area to area anterior to mouthparts, these setae becoming progressively longer towards mouthparts. Ventral microducts present in groups of 10–20 on area between each antenna and eye, and between each anterior spiracle and body margin, absent elsewhere. Multilocular pores each 4–6 μm in diameter, with 3–8 (mostly 5) loculi; present on mid areas of abdominal segments, with a few pores on thorax around hind coxae. Spiracular pores each 3–4 μm in diameter.

Etymology. The species epithet "*viridis*" is derived from the Latin meaning green, after the color of the young insect in life.

Diagnosis. *Intecticoccus viridis* can be distinguished from other species of eriococcids by the following combination of features: (i) a bare dorsum, not covered by a felted cover, (ii) the very small dorsal and marginal setae, each 3–7 μm long, (iii) claws without denticle, and (iv) the lack of bilocular pores on the dorsum and venter. *I. viridis* appears most similar to *Icelococcus charlini* Miller & González and *Chilechiton lynnae* due to the absence of dorsal macroducts. *Intecticoccus viridis* differs from both in: (i) having all

dorsal setae evenly short (large-sized setae present on medial area in *I. charlini*; all enlarged on *C. lynnae*), (ii) lack of a small accessory plate at the anterior base of sclerotized anal lobes (present on *I. charlini* and *C. lynnae*); (iii) translucent pores minute on hind coxae (rather large on *I. charlini* and *C. lynnae*) and in (iv) the lack of claw denticles (present on *I. charlini* and *C. lynnae*).

Orafortis Hardy gen. nov.

Type species: Orafortis luma Hardy, sp. nov., by present designation.

Generic description of adult female

Live appearance: Insect ovate, concealed within spiky test.

Mounted material: Eyespots on venter. Antennae 6-segmented. Labium 3-segmented, basal segment indicated only by presence of setae; with 7 pairs of setae. Legs well developed; translucent pores present as sclerotic pits, restricted to dorsal surface of hind coxae. Anal lobes sclerotic, subconical, inner margin crenulate, with acute constriction just distal of medial lobe seta. Anal ring bearing 8 setae and 2 rows of pores. Suranal setae spinose.

Dorsum: Derm nodulose, nodules becoming sclerotic caudad. Setae conical, varying considerably in size. Macrotubular ducts of 2 size classes, both with distinct sclerotic rims around dermal orifice, rim of smaller macrotubular duct much wider than diameter of duct shaft; smaller ducts distributed similar to setae; larger ducts dilated towards inner ductule, present around body margins. Microtubular ducts with distinct septum, most dorsal setae with 1–3 microtubular ducts opening at base, plus a few microtubular ducts on dorsal surface of each anal lobe. Multilocular pores absent.

Venter: Derm membranous; abdominal microtrichia becoming strongly developed towards margins in areas occupied by spinose setae on abdomen and thorax. Ventral setae present, flagellate on mid venter; short spinose along submargin. Macrotubular ducts similar to smaller ducts on dorsum, scattered across all segments. Microtubular ducts absent. Multilocular pores mostly with 5-loculi. Bilocular pores absent.

Diagnostic comments. Orafortis is the only known South American eriococcid genus to have microtubular ducts opening at the bases of the enlarged dorsal setae. The distinct sclerotized rims surrounding the dermal opening of each tubular duct are also diagnostic. Two other genera, Exallococcus Miller & González and Stibococcus Miller & González, also have ducts with distinct oral rims but, in these two genera, the oral rims are broad and rather unevenly thickened, in contrast to the oral rims of Orafortis that are thin but evenly solid. Furthermore, the much greater diameter of the oral rim compared to the diameter of the duct shaft is unique. Orafortis differs from Exallococcus in having neither bilocular pores nor a medial plate just anterodorsal of the anal ring. Orafortis differs from Stibococcus in having sclerotic anal lobes and far fewer ventral multilocular pores, which

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are not organized into distinct clusters.

Etymology. The genus name is formed by compounding "ora", the Latin term meaning "rim", with *fortis*, the Latin word meaning "strong". The name refers to the thickened and conspicuous dermal oral rim surrounding the opening of each tubular duct.

Orafortis luma Hardy sp. nov. (Figs 2C, 4)

Type material. HOLOTYPE, adult female. **CHILE**: X Region, Parque Nacional Alerce Andino, 41°27′52″ S, 72°38′42″ W, 120 m, 19.ii.2006, coll. T. Kondo, ex test on twig of *Amomyrtus luma* (MNNC). **PARATYPES**: **CHILE**: same data as holotype, 13 adult females (6 BME + 2 BMNH + 2 MNNC + 2 USNM), 5 first-instar nymphs (in poor condition) on 1 slide (BME).

Description of adult female (n = 14)

Live appearance. Insect concealed within spiky test, ca. 2 mm long, ca. 1 mm wide, cryptic upon hirsute stems and leaf or stem axils of host (Fig. 2C). Test comprised of numerous glassy filaments, 0.2–0.4 mm long, arising from tightly-woven matrix, with rounded anal opening ca. 0.3 mm in diameter. Test of the male ca. 1.5 mm long, occurring on underside of leaves.

Mounted material. Body outline ovate (Fig. 4), 1.30-1.64 mm long, 0.90-1.08 mm wide. Eyespot 20 μm wide. Antennae 205–215 μm long; 3 hair-like setae (trichoid sensilla) on segment I, 2 hair-like setae on segment II, 3 hair-like setae on segment III, 1 fleshy seta on segment IV, 4 hair-like setae and 1 fleshy seta on segment V, about 6 hairlike setae and 3 fleshy setae on segment VI. Tentorial box 125–150 µm long, 120–137 µm wide. Labium 75–88 μm long, 75–87 μm wide across base, with 7 pairs of setae: 1 pair on basal segment, 1 pair on medial segment, and 5 pairs on apical segment (including minute apical setae). All legs with trochanter + femur 122–137 µm long, tibia + tarsus 147–175 μm long; tarsal digitules 40–50 μm long, claw digitules 25–30 μm long, all digitules slender with moderately expanded apices, 2 µm wide; claw denticle present; translucent pores present as heavily sclerotized pits with either small circular or irregular slit-like openings 1-10 µm long, 5-10 pores on dorsal surface of each hind coxa; microtrichia on ventral side of all coxae. Spiracular peritremes: mesothoracic 20-22 µm wide; metathoracic 25–30 µm wide. Anal lobes: dorsolateral lobe seta 32–37 µm long, dorsomedial lobe seta 52-55 μm long, dorsoapical lobe seta 60-65 μm long, caudal seta 117–125 μm long, ventral lobe seta 50–55 μm long. Anal ring 125–150 μm long, 50–55 μm wide. Suranal setae 70–80 μm long.

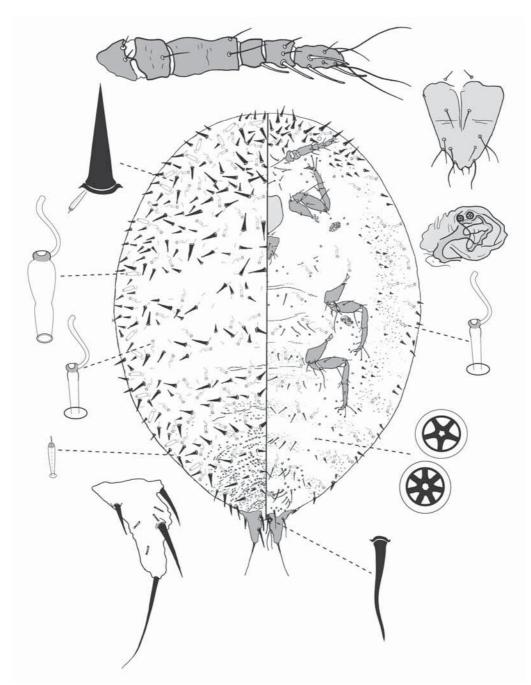


FIGURE 4. Adult female of *Orafortis luma* Hardy **sp. nov.** (anal ring concealed by the anal lobes and not drawn as an enlargement).

Dorsum: Setae conical, each seta 22–70 μ m long; arranged in transverse rows across each body segment, rows increasingly irregular cephalad. Macrotubular ducts of 2 size classes; smaller ducts about 25 μ m long, 4 μ m wide, with distinct dermal rim around orifice, 5–7 μ m in diameter, distributed similar to setae, in transverse rows across body

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segments, more numerous and irregularly placed cephalad; larger ducts about 30 μ m long, dilated near inner ductule, ca. 10 μ m wide, dermal orifice sclerotic, 6 μ m in diameter; in a marginal series. Microtubular ducts, about 15 μ m long, orifice 1–2 μ m in diameter; scattered across dorsum, with 1–3 opening at base of each dorsal seta, plus about 4 on dorsal surface of each anal lobe.

Venter: Flagellate setae each 20–60 μm long; in transverse row across medial portion of abdominal segments I–VII, plus a few medial to each coxa and a number in a paired longitudinal series extending from scape to tentorial box; short spinose setae, 8–15 μm long. Macrotubular ducts scattered across all segments. Multilocular pores 5 μm in diameter, most with 5 loculi, a few with 7 loculi; distributed across all body segments, with weak concentrations on submedial areas of each abdominal segment and near spiracles but not forming a group between spiracles and margin; also with 2–5 incorporated into each sclerotic spiracular peritreme.

Etymology. The species epithet "*luma*", a noun in apposition, is derived from the host plant: *Amomyrtus luma*.

Diagnosis. Orafortis luma appears superficially similar to Eriococcus Targioni Tozzetti sensu lato species but can be distinguished from all Eriococcus species described from Chile by (i) the distinct sclerotic rim around the dermal orifice of the macrotubular ducts, (ii) sclerotic nodules on dorsal surface of posterior abdominal segments, (iii) microtubular ducts opening at bases of enlarged dorsal setae, and (iv) two size classes of dorsal macrotubular ducts. Only three species of Eriococcus are known from species of Myrtaceae in South America (Miller & Gimpel 2000; Ben-Dov et al. 2006): E. jorgenseni Morrison from Psidium (and perhaps also from Myricaceae) in Argentina (Morrison 1919), E. lanatus Hempel from Eugenia in Brazil (Hempel 1932), and E. perplexus Hempel from Eugenia and Myrciaria in Brazil (Hempel 1900; Miller & Gimpel 2000). O. luma can be distinguished from E. jorgenseni by (i) the variable size, and acute apices of the dorsal setae (all dorsal setae are approximately the same size and have rounded apices in E. jorgenseni), (ii) 6-segmented antennae (7-segmented in E. jorgenseni) and (iii) only 5-10 translucent pores on each hind coxa (ca. 40 large pores in E. jorgenseni). O. luma differs from E. lanatus in the following: (i) test with a distinct anal orifice (no anal orifice detected in E. lanatus), (ii) antennae 6-segmented (7-segmented in E. lanatus), (iii) only 5–10 translucent pores on each hind coxa (40 or more visible on hind legs of E. lanatus), and (iv) all legs not thickened. E. perplexus also has 7-segmented antennae and all legs thickened and further differs from O. luma by having only 6 anal ring setae. O. luma can be distinguished from all Chilean Eriococcus species as indicated in couplet 7 of the following key.

Notes on the first-instar nymphs of *Orafortis luma* sp. nov. (n = 5)

The specimens were poorly cleared and a complete description was impossible, but the following features should be diagnostic. Body length 440–495 μ m, maximum width 220–295 μ m. Dorsal surface of abdominal segments with 4 longitudinal rows of setae; submedial setae uniformly blunt and knob-like, ca. 3 μ m long, medial setae like submedial



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setae on anterior abdominal segments, increasing in length caudad, ca. 12 μ m long on abdominal segment VII. Microtubular ducts opening at bases of the marginal setae, at least on posterior abdominal segments. Setae on ventromedial portions of posterior abdominal segments unusually robust and elongate, ca. 35 μ m long.

Revised key to adult females of the Eriococcidae of Chile

(Modified from Miller & González 1975; Hodgson & Miller 2002).

1.	Macrotubular ducts absent from dorsum
-	Macrotubular ducts present on dorsum
2.	Plate-like anal lobes withdrawn onto dorsal surface at anterior end of anal cleft; sur-
	face of anal lobes with conspicuous translucent areas, each with a well defined C-shape or irregular margin
-	Plate-like anal lobes present apically; surface of lobes without conspicuous translucent areas
3.	Inner margins of plate-like anal lobes without teeth; triangular plate absent on dorsum anterior to plate-like anal lobes; bilocular pores absent
-	Inner margins of plate-like anal lobes with many medial teeth; triangular plate present
	on dorsum anterior to plate-like anal lobes; bilocular pores present4
4.	Hind coxae without translucent pores; dorsal setae of one size only
-	Hind coxae with translucent pores; dorsal setae of 2 sizes
5.	Macrotubular ducts present on venter; hind coxae not greatly expanded
-	Macrotubular ducts absent on venter; hind coxae greatly expanded
6.	Macrotubular ducts on dorsum each with large, conspicuous, often sclerotized rim around dermal orifice
-	Macrotubular ducts on dorsum without large, conspicuous, often sclerotized rim around dermal orifice
7.	Enlarged dorsal setae with microtubular ducts opening at their base; larger macrotubular ducts dilated near inner ductule; dorsal surface of posterior abdominal segments sclerotic in mature specimens
-	Dorsal setae without microtubular ducts opening at their base; macrotubular ducts without dilations near inner ductule; dorsal surface of only abdominal segment VIII sclerotic, or all segments membranous
8.	Venter with large clusters of macrotubular ducts on abdomen; dorsum without simple
٥.	pores; without bilocular pores
-	Venter without macrotubular ducts on abdomen; dorsum with numerous simple pores; bilocular pores present on venter near body margin

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9.	Enlarged setae abundant ventrally on all areas of abdomen; anal lobes sclerotized and plate-like
-	Enlarged setae not abundant, when present, restricted to lateral areas of venter of abdomen; anal lobes unmodified, not plate-like
10.	Multilocular pores abundant on dorsum as well as mediolateral and lateral areas of venter; dorsal surface of each hind coxa with 35–65 pores
-	Multilocular pores absent from dorsum, restricted to narrow longitudinal band on mediolateral areas of venter; dorsal surface of each hind coxa with 65–120 pores C. browni Miller & González
11.	Dorsal setae each dome-shaped; hind femora each with 4 setae
-	Dorsal setae not dome-shaped; hind femora with 5 setae
12.	Suranal setae spatulate; femora of front legs each with 6 setae
- 13.	Suranal setae bristle-shaped; femora of front legs each with fewer than 6 setae 13 Dorsomedial enlarged setae each truncate apically; ventral multilocular pores on thorax of one size, each usually with 3 loculi; tibiae of front legs each with 5 setae E. araucariae Maskell
-	Dorsomedial enlarged setae each with an acute or rounded apex; ventral multilocular pores on thorax of two sizes, each usually with 5 loculi; tibiae of front legs with 4 setae
14.	Dorsomedial setae on abdomen each about equal in length to largest lateral setae Eriococcus chilensis Miller & González
-	Dorsomedial setae on abdomen each noticeably smaller than largest lateral setae $\dots 15$
15.	Dorsal surface of abdominal segment V with 9–14 enlarged setae; enlarged setae on dorsomedial areas of thorax and head each about as long as those along margin of abdomen
-	Dorsal surface of abdominal segment V with 19–31 enlarged setae; enlarged setae on dorsomedial areas of thorax and head each noticeably shorter than those along margin of abdomen

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References

- Ben-Dov, Y., Miller, D.R. & Gibson, G.A.P. (2006) *ScaleNet: a Database of the Scale Insects of the World*. Scales in a Region Query Results. Available from http://www.sel.barc.usda.gov/SCALE NET/SCALENET.HTM (accessed 21 March and 9 July 2006).
- Cox, J.M. & D.J. Williams (1988). Do the Eriococcidae form a monophyletic group? *Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri*' (1986), 43, 13–17.
- Cook, L.G. & Gullan, P.J. (2004) The gall-inducing habit has evolved multiple times among the eriococcid scale insects (Sternorrhyncha: Coccoidea: Eriococcidae). *Biological Journal of the Linnean Society*, 83, 441–452.
- Cook, L.G., Gullan, P.J. & Trueman, H.E. (2002) A preliminary phylogeny of the scale insects (Hemiptera: Sternorrhyncha: Coccoidea) based on nuclear small-subunit ribosomal DNA. *Molecular Phylogenetics and Evolution*, 25, 43–52.
- Gibbs, RA, & Cockerill, M. (1995) Sequencher. 3.0 ed. Ann Arbor: Gene Codes Corporation.
- González, P. (2000) First record of the genera *Chilecoccus* and *Icelococcus*, and two *Acanthococcus* species (Hemiptera: Eriococcidae) for Argentina. *Revista de la Sociedad Entomologica Argentina*, 59, 51–52.
- Gullan, P.J. (1984) A revision of the gall-forming coccoid genus *Apiomorpha* Rübsaaman (Homoptera: Eriococcidae: Apiomorphinae). *Australian Journal of Zoology, Supplementary Series* No. 97, 1–203.
- Gullan, P.J., Giliomee, J.H., Hodgson, C.J. & Cook, L.G. (2006) The systematics and biology of the South African gall-inducing scale insect, *Calycicoccus merwei* Brain (Hemiptera: Coccoidea: Eriococcidae). *African Entomology*, 14, 13–33.
- Gullan, P.J., Miller, D.R. & Cook, L.G. (2005) Gall-inducing scale insects (Hemiptera: Sternorrhyncha: Coccoidea). In: Raman, A., Schaefer, C.W. & Withers, T.M. (Ed.), *Biology, Ecology, and Evolution of Gall-Inducing Arthropods*. Science Publishers, Inc., Enfield, USA, Plymouth, UK, pp. 159–229.
- Gullan, P.J. & Strong, K.L. (1997) Scale insects under eucalypt bark: a revision of the Australian genus *Phacelococus* Miller (Hemiptera: Eriococcidae). *Australian Journal of Entomology*, 36, 229–240.
- Gullan, P.J. & Vranjic, J.A. (1991) The taxonomy of the gum tree scales *Eriococcus confusus* Maskell and *E. coriaceus* Maskell (Hemiptera: Coccoidea: Eriococcidae). *General and Applied Entomology*, 23, 21–40.
- Hempel, A. (1900) [Brazilian coccids.] As coccidas Brasileiras. *Revista do Museu Paulista. São Paulo*, 4, 365–537.
- Hempel, A. (1932) [Descriptions of 22 new species (Hemiptera Homoptera).] Descripção de vinte a duas espécies novas de coccideos (Hemiptera Homoptera). *Revista de Entomologia*, 2, 310–339.
- Henderson, R.C. (2006) Four new species and a new monotypic genus *Hoheriococcus* (Hemiptera: Coccoidea: Eriococcidae) associated with plant galls in New Zealand. *New Zealand Entomologist*, 29, 37–57.
- Hodgson, C.J. (1994) Eriochiton and a new genus of the scale insect family Eriococcidae



- (Homoptera: Coccoidea). Journal of the Royal Society of New Zealand, 24, 171-208.
- Hodgson, C.J. (2002) Preliminary phylogeny of some non-margarodid Coccoidea (Hemiptera) based on adult male characters. *Bollettino di Zoologia agraria e di Bachicoltura*, Ser. II, 33, 129–137.
- Hodgson, C.J. & Henderson, R.C. (1996) A review of the *Eriochiton spinosus* (Maskell) speciescomplex (Eriococcidae: Coccoidea), including a phylogenetic analysis of its relationships. *Journal of the Royal Society of New Zealand*, 26, 143–204.
- Hodgson, C.J. & Miller, D.R. (2002) A new genus and two new species of felt scales (Hemiptera: Coccoidea: Eriococcidae) from Chile, with comments on zoogeographical affinities between the eriococcid faunas of southern South America and New Zealand. Systematic Entomology, 27, 191–209.
- Hoy, J.M. (1962a) Eriococcidae (Homoptera: Coccoidea) of New Zealand. New Zealand Department of Scientific and Industrial Research Bulletin, 146, 1–219.
- Hoy, J.M. (1962b) A new species of *Eriococcus* from Navarino Island, Tierra del Fuego. *New Zealand Journal of Science*, 5, 510–512.
- Kondo, T., Gullan, P.J., and Miller, D.R. (2004) A new hypogeal species of *Oregmopyga* Hoy (Hemiptera: Coccoidea: Eriococcidae) from southern California, U.S.A., and a key to species of the genus. *Zootaxa*, 784, 1–12. http://www.mapress.com/zootaxa/2004f/zt00784.pdf
- Landrum, L.R. (1988) The myrtle family (Myrtaceae) in Chile. *Proceedings of the California Academy of Sciences*, 45, 277–317.
- McQuillan, P.B. (1993). *Nothofagus* (Fagaceae) and its invertebrate fauna an overview and preliminary synthesis. *Biological Journal of the Linnean Society*, 49, 317–354.
- Miller, D.R. & Gimpel, M.E. (2000) A Systematic Catalogue of the Eriococcidae (Felt Scales) (Hemiptera: Coccoidea) of the World. Intercept Ltd., Andover, U.K., 589 pp.
- Miller, D.R. & Gimpel, M.E. (2006) *ScaleNet*. Eriococcidae. Available from http://www.sel.barc.usda.gov/SCALENET/SCALENET.HTM (accessed 21 March and 9 July 2006).
- Miller, D.R. & González, R.H. (1975) A taxonomic analysis of the Eriococcidae of Chile. *Revista Chilena de Entomología*, 9, 131–163.
- Miller, D.R. & McKenzie, H.L. (1967) A systematic study of *Ovaticoccus* Kloet and its relatives, with a key to North American genera of Eriococcidae (Homoptera: Coccoidea: Eriococcidae). *Hilgardia*, 38, 471–539.
- Morrison, H. (1919) A report on collection of Coccidae from Argentina, with descriptions of apparently new species (Hom.). *Proceedings of the Entomological Society of Washington*, 21, 63–91.
- Rambaut, A. (1996) Se-Al: Sequence Alignment Editor. Available from http://evolve.zoo.ox.ac.uk/ Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
- Sytsma, K.J., Litt, A., Zjhra, M.L., Pires, J.C., Nepokroeff, M., Conti, E., Walker, J. & Wilson, P.G. (2004) Clades, clocks, and continents: historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the southern hemisphere. *International Journal of Plant Sciences* 165, S85–S105.
- Tautz, D., Hancock, J.M., Webb, D.A., Tautz, C., & Dover, G.A. (1988) Complete sequences of the rRNA genes of *Drosophila melanogaster*. *Molecular Biology and Evolution*, 5, 366–376.
- Veblen, T.T., Hill, R.S. & Read, J. (Ed.) (1996) *The Ecology and Biogeography of Nothofagus Forest*. Yale University Press, New Haven, CT.
- von Dohlen, C.D. & Moran N.A. (1995) Molecular phylogeny of the Homoptera: a paraphyletic taxon. *Journal of Molecular Evolution*, 41, 211–223.
- Williams, D.J. (1985) The British and some other European Eriococcidae (Homoptera: Coccoidea). *Bulletin of the British Museum (Natural History), Entomology Series,* 51, 347–393.
- Zuloaga, F.O. & Morrone, O. (Ed.) (1999) Catálogo de las Plantas Vasculares de la República Argentina II. Missouri Botanical Garden Press, St Louis.